Ecological Indicators 115 (2020) 106400

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

# Rapid assessment of avian species richness and abundance using acoustic indices

Tom Bradfer-Lawrence[a,*], Nils Bunnefeld[a], Nick Gardner[a], Stephen G. Willis[b], Daisy H. Dent[a,c]

[a] Biological & Environmental Sciences, University of Stirling, UK
[b] Conservation Ecology Group, Department of Biosciences, Durham University, Durham, UK
[c] Smithsonian Tropical Research Institute, Panama City, Panama

ARTICLE INFO

*Keywords:*
Birds
Conservation
Ecoacoustics
Monitoring
Sound recording
Soundscape

ABSTRACT

Accelerating global shifts in climate and land use change are altering natural habitats and species assemblages, making management interventions crucial to halt the biodiversity crisis. Management decisions must be informed by accurate biodiversity assessments. However, such assessments are often time consuming, expensive, and require specialist knowledge. Monitoring environmental sound may offer a novel method for rapid biodiversity assessment. Changes in species assemblages at a given location are reflected in the site's acoustic energy, termed the soundscape. Soundscapes can be readily described using acoustic indices; metrics based on objective features of recordings such as pitch and amplitude. Changes in acoustic indices values may therefore reflect changes in species assemblages, alerting land managers to shifts in wildlife populations. However, thus far, evidence supporting the use of acoustic indices in biodiversity monitoring has been equivocal. Here, we test the practical application of acoustic indices for biodiversity monitoring while solving methodological issues and providing conceptual clarity.

Using 84 h of audio recordings covering 315 dawns from 43 sites, coupled with bird assemblage and vegetation data collected in the field, we demonstrate strong relationships between acoustic indices and avian species richness and abundance. In contrast with many previous studies, we found that sites with high bird species-richness and abundance had less even soundscapes (i.e. acoustic energy was less evenly distributed among frequencies) compared with sites with low species richness and abundance. Crucially, these patterns were coherent across multiple acoustic indices, and across habitat types, emphasising their utility for monitoring. Acoustic indices sensitive to the frequencies at which birds sing are most useful for monitoring avian communities; the Acoustic Evenness Index, Biophony Index, and the biophony component of the Normalised Difference Soundscape Index exhibited the strongest relationship with species richness. Land managers can use acoustic indices for biodiversity monitoring, complementing other, more established, assessment methods.

## 1. Introduction

Biodiversity assessment is an increasingly urgent task in the face of global environmental change (Pereira et al., 2013). Ecoacoustics, the study of environmental sound, may offer a more rapid and economical means of terrestrial biodiversity appraisal than traditional approaches (Burivalova et al. 2019a). Cheap, open-source audio recorders that can be deployed in the field for weeks or months at a time have made it relatively straightforward to collect tens of thousands of hours of sound recordings (Sueur and Farina 2015; Bradfer-Lawrence et al. 2019). Acoustic indices can be calculated from audio recordings, rather than manually categorising species composition, which is prohibitively time-consuming (Pijanowski et al. 2011). Acoustic indices are derived from features of the recordings such as amplitude and frequency, with individual indices typically describing different characteristics of the soundscape (Sueur et al. 2014). The soundscape is comprised of the acoustic energy at a given location and has three components: biophony, sounds produced by animals; anthrophony, sounds produced by humans or machinery; and geophony, sounds from natural processes such as wind or rain (Pijanowski et al 2011).

Any changes to a habitat and its fauna are likely to be mirrored in the local soundscape (Krause and Farina, 2016; Burivalova et al. 2018; Gómez et al. 2018; Bradfer-Lawrence et al. 2019; Furumo and Aide, 2019). In turn, these will be echoed in changing acoustic indices values reflecting differences in biophony and geophony. If acoustic indices values change in consistent and predictable ways as a response to

* Corresponding author.
*E-mail address:* tom.bradfer-lawrence@stir.ac.uk (T. Bradfer-Lawrence).

https://doi.org/10.1016/j.ecolind.2020.106400
Received 17 November 2019; Received in revised form 26 February 2020; Accepted 8 April 2020

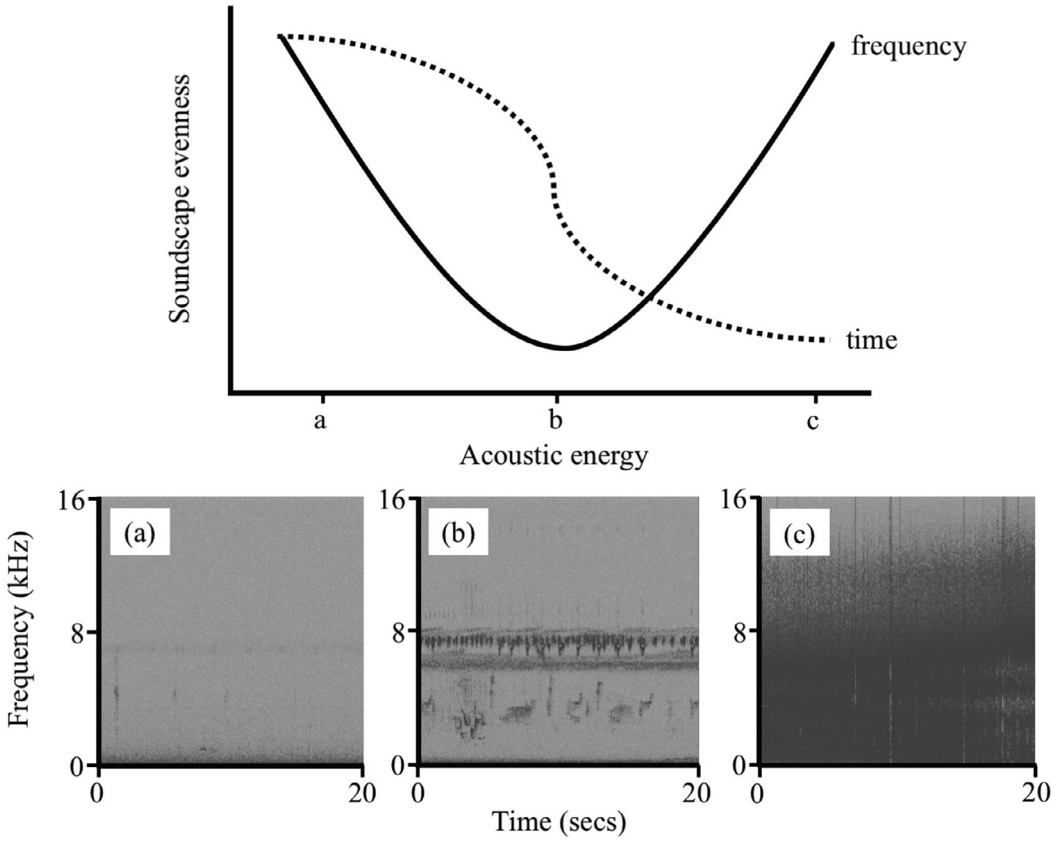


**Fig. 1.** Soundscape changes with increasing acoustic energy. At top, a hypothetical graph showing changes in soundscape evenness for frequency (solid line) and time (dotted line), and below, example sonograms from three recordings collected in central Panama in March 2017 at around 06:30 am. Panel (a) shows a sonogram from a scrub recording, with only two bird calls and low levels of insect noise. There are low levels of acoustic energy and the soundscape is very even, with little temporal or frequency variation. Panel (b) shows a sonogram from a forest recording, bird calls dominate frequencies between 1 and 6kHz, and insects between 6 and 8 kHz. Above 9 kHz there are few sounds, so that acoustic energy is unevenly distributed among frequency bands, reflecting the complex faunal communities present in this habitat. Panel (c) shows a sonogram from a rainstorm, there are high levels of acoustic energy and high temporal variation in the soundscape, but little differentiation among frequency bands. Thus soundscapes with low or high amounts of acoustic energy (panels a and c) may be different temporally, but generally have low variation among frequencies. At intermediate levels of energy (panel b), there is considerable temporal and frequency variation in the sonogram, so that the soundscape is uneven. Each recording will have a unique combination of indices values, reflecting soundscape variation. Excepts from these and other example recordings are available in the supplementary information.

shifting vegetation structure and species assemblages, indices could be used as proxies for tracking such alterations and hence represent an economical means of monitoring biodiversity change across both space and time at large scales (Bradfer-Lawrence et al. 2019; Laiolo 2010; Ribeiro et al. 2017).

To illustrate how acoustic patterns can reflect biodiversity, Fig. 1 shows three sonograms of tropical dawn recordings with contrasting soundscapes. Patterns in acoustic energy vary in two ways: among frequencies and over time. One recording was collected in regenerating scrub habitat with low avian species richness (Fig. 1a). There are few calling birds and low acoustic energy, and hence minimal variation across frequencies or time. In contrast, Fig. 1b shows a recording from a large area of forest with a more complex vegetation structure and high avian species richness, features that are echoed in a highly uneven soundscape typified by rapid temporal irregularity and variation in acoustic energy among frequencies. Here, the dawn chorus contains numerous individuals of many species vocalising simultaneously between 1 and 10 kHz, but with few sounds outside this range. Fig. 1c shows a recording collected during a rainstorm, a soundscape with high levels of acoustic energy and high temporal variation, but with the same minimal variation among frequency bands found in the scrub recording. Acoustic indices will reflect these differences, with a distinct combination of values for each soundscape, and values for the forest recording (Fig. 1b) indicating a soundscape with less even distribution of energy among frequency bands compared to the other two recordings.

Realising the potential of acoustic indices for monitoring biodiversity change relies on significant and coherent relationships between acoustic indices and widely used biodiversity metrics such as species richness. However, there are currently disagreements as to the strength and direction of such relationships. For example, the Acoustic Complexity Index (ACI) has been correlated positively with both avian species richness (Hilje et al. 2017) and peaks in avian vocalisations (Farina et al. 2011; Pieretti et al. 2011; Fuller et al. 2015; Gage et al. 2017). In contrast, other studies have found no relationship between ACI and avian species richness (Fuller et al., 2015; Buxton et al., 2016, 2018a,b). Similarly, while a strong positive correlation between the Biophony index (Bio) and avian abundance has been found by some (Boelman et al. 2007; Fuller et al. 2015), others report the reverse (Gage et al. 2017). Some of these disagreements may have arisen from a failure to consider the influence of vegetation. Vegetation might influence acoustic indices values directly, by affecting sound transmission (Darras et al., 2016), or indirectly by shaping the animal populations present in an area (Burivalova et al 2018). Vegetation effects on the soundscape can be strong; simplified vegetation structure is associated with lower soundscape saturation and lower Bio values indicating greater evenness among frequencies (Rankin and Axel, 2017; Burivalova et al., 2019b, Burivalova et al., 2018).

The inconsistent patterns between species metrics and acoustic indices raise questions regarding the efficacy of indices for biodiversity assessment (Servick 2014; Merchant et al. 2015; Eldridge et al. 2016; Browning et al. 2017; Gibb et al. 2018). This is likely limiting uptake of these new technologies by land managers. We suggest there are several conceptual and methodological issues that underlie the reported inconsistencies, and these may be obscuring relationships between soundscapes, landscapes and biodiversity. Key amongst these limitations is the use of acoustic indices without a solid *a priori* understanding of the likely relationships between indices values and biodiversity. Apparent relationships have been reported because they were statistically significant, without the trends necessarily making ecological sense or inter-index patterns being complimentary. For example, some studies suggest that greater avian species richness is associated with higher evenness among frequencies (Fuller et al. 2015; Mammides et al. 2017), but this is unlikely unless all frequencies are occupied equally (Fig. 1, and Eldridge et al 2018).

Conceptual weaknesses have been compounded by inconsistent or inappropriate methodologies. For example, while the bird assemblage contributes to the overall soundscape, there is likely to be considerable short-term variation. Calls are irregular within and among bird species, and affected by the animal's distance from the microphone, by habitat structure, and by other sources of biophony and geophony (Lellouch et al 2014). With so much soundscape variability a direct relationship between bird assemblages and acoustic indices is unlikely, hence attempts to link acoustic indices with concurrent avian counts have met with limited success (Lellouch et al. 2014; Mammides et al. 2017; Buxton et al. 2018b; Eldridge et al. 2018; Jorge et al. 2018; Zhao et al. 2019). Clearer trends might be apparent if acoustic indices were treated as site metrics more akin to net primary productivity. Furthermore, analysis techniques have frequently been limited to linear regressions or non-parametric statistics (Boelman et al. 2007; Tucker et al. 2014; Duarte et al. 2015; Mammides et al. 2017). Yet index values are often highly skewed, exhibiting non-normal error distributions, thus a more nuanced approach to analyses is probably required (Fairbrass et al 2017).

The principal question we address is: can acoustic indices be used as effective biodiversity monitoring tools, reflecting species richness and abundance? We hypothesise that greater avian species richness, avian abundance, and vegetation structural complexity will be reflected in acoustic indices values indicating greater soundscape complexity. We designed our study to avoid many of the issues that have limited earlier studies, treating indices as site characteristics and employing advanced analytical techniques. We consider a suite of well-established acoustic indices from week-long recordings collected from 43 sites with a range of vegetation types and varied avifaunas, and couple these recordings with over 126 h of avian point count observations from the same sites.

## 2. Materials and methods

This study was conducted in the Emparador landscape in the Republic of Panama. This human-modified landscape lies to the south and west of the Panama Canal, covering 700 km$^2$. Whilst there are still extensive tracts of forest, large areas have been converted to a matrix of cattle pasture and teak plantation, with remnant forest fragments and riparian forest. The climate is strongly seasonal, with very low rainfall between mid-December and mid-April, while the wet season generally peaks in October and November (Windsor 1990).

### 2.1. Data collection and preparation

Data were collected in 2017 from 43 sites representing the six main habitats present in the Emparador landscape; continuous forest, fragmented forest, riparian forest, teak plantations, regenerating scrub and cattle pasture (Fig. 2). Sites were of uniform habitat, a minimum of 1 ha in size, and at least 500 m from sites in other habitats and 1000 m from sites of the same habitat. Habitats followed a hypothesised gradient of decreasing structural complexity from continuous forest to cattle pasture.

### 2.2. Audio recordings

Audio recordings were collected using open-source "Solo" recorders with omnidirectional microphones (Whytock and Christie, 2017). We opted for a sampling rate of 32,000 Hz as a balance between capturing the majority of human-audible sound and the memory capacity of the recorders (Bradfer-Lawrence et al. 2019). Collection was limited to the dry season (early February to early May), when bird song makes a relatively greater contribution to the soundscape. Recorders were deployed for approximately one week at each site (range 6 – 11 days), deployment length was determined by how long the recorder battery retained power. This gave a total of 315 deployment days, from which we extracted data for the minute of sunrise and the following 15 min for each morning (sunrise times from timeanddate.com). This corresponded to the period with the greatest level of birdsong, and gave a total of 5040 min of analysis (between 96 and 176 min of recording per site). We did not screen recordings for high levels of geophony (wind and rain). Pre-processing was limited to a 500 Hz low-stop filter to reduce microphone self-noise. This filter likely removed some genuine environmental sound, but the self-noise represented a potential source of bias in the indices that needed to be controlled for (Appendix A).

For each minute of recording we calculated the following acoustic indices; Acoustic Complexity Index (ACI), Acoustic Diversity Index (ADI), Acoustic Evenness Index (AEve), Biophony Index (Bio), Acoustic Entropy Index (H), Amplitude (M), Normalised Difference Soundscape Index (NDSI), and the latter's two constituents reflecting anthrophony and biophony (given the potential for diverging patterns in the two elements of NDSI, they were considered separately). Details of index calculation and the general patterns they reflect can be found in Appendix B. Over 60 acoustic indices have been proposed (Buxton et al., 2018a), but we focused on these nine indices because they are the most commonly used in the acoustic indices literature, and they capture a range of soundscape characteristics. All indices were calculated in R, using the packages 'seewave' (ver 2.1.0; Sueur et al., 2008) and 'soundecology' (ver 1.3.3; Villanueva-Rivera and Pijanowski, 2018). The default values of each R function were used, with the exception of NDSI which was modified to match the original formulation of Kasten et al (2012). In the original form, this index contrasts the power spectral density of the 1 kHz anthrophony bin (i.e. 1 – 2 kHz), against the power spectral density of the *largest* 1 kHz biophony bin (i.e. in the range 2 – 11 kHz). However, both the 'seewave::NDSI' and 'soundecology::ndsi' functions use an alternative method where the biophony bins are summed prior to this calculation. This tends to obscure differences among recordings; for a full discussion see Appendix C.

### 2.3. Bird assemblages

Bird assemblages at each site were assessed in the field using 10-min, unlimited radius point counts (Bibby et al. 2000). We conducted four visits to each of the 43 sites, giving a total of 172 counts. Counts were undertaken between 30 min after morning nautical twilight and 4 h post-dawn. Revisits to sites were a minimum of 12 days apart. All counts were undertaken by TBL and NG. Double counting of individuals during surveys was highly unlikely given the minimum distance between sites. We recorded all birds seen or heard with the exception of vultures, hirundines and swifts; these three taxa are predominantly aerial in behaviour, so their presence may not reflect usage of the habitat being surveyed. We did not modify our counts based on detectability; hence, our data reflect relative site features rather than absolute measures of bird abundance (Anderson 2009). For each site we calculated mean bird species richness and mean number of individuals detected based upon sightings and vocalisations. We used the latter as our

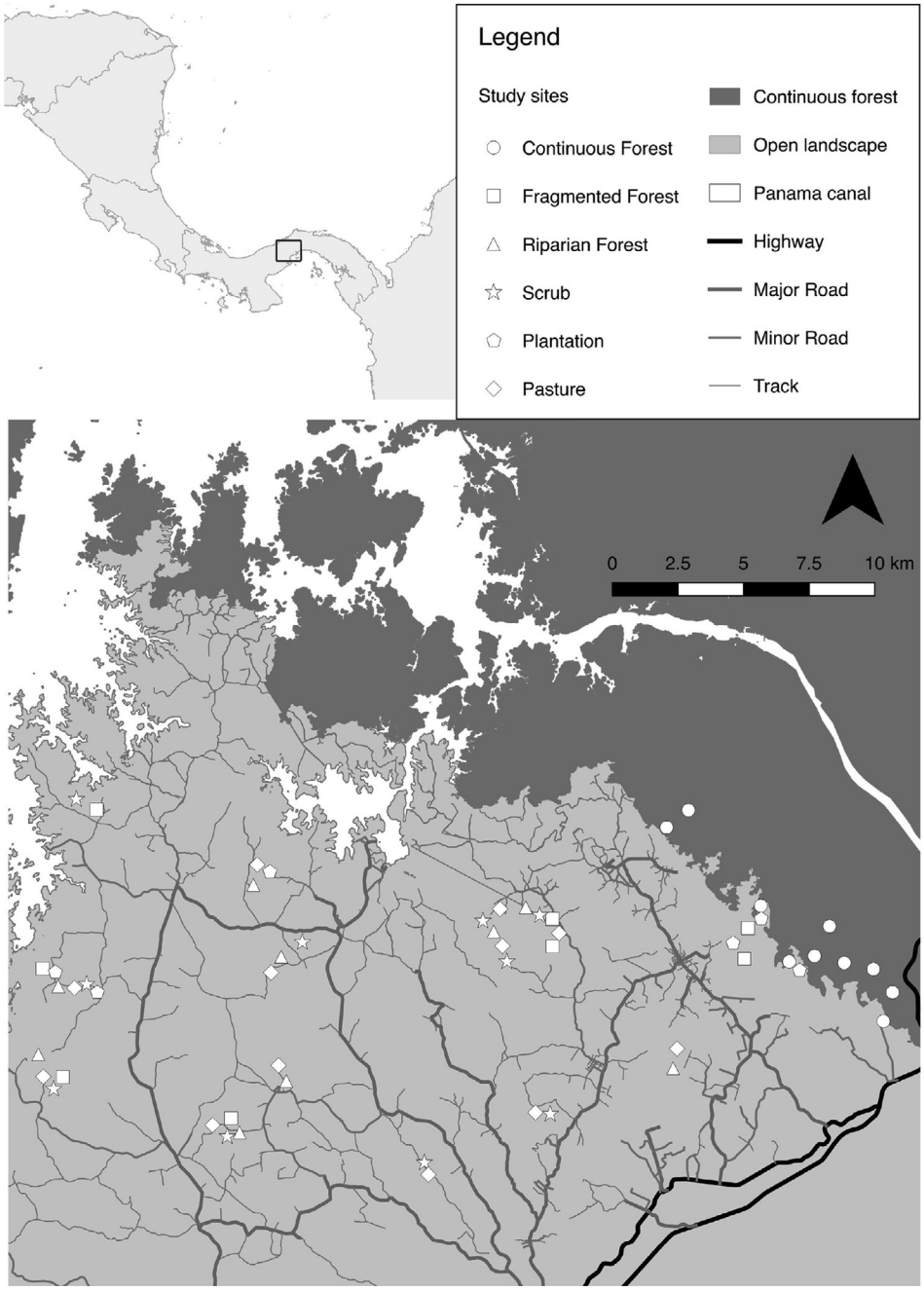


**Fig. 2.** Map of 43 study sites in the Emparador landscape, central Republic of Panama, showing the six habitat types.

proxy for avian abundance. These two metrics were used as predictors in the modelling (see below).

### 2.4. Vegetation data

Woody vegetation at each site was assessed with a 20 m × 20 m plot. We recorded: canopy height at nine points, number of stems over 1.3 m tall, and Diameter at Breast Height (DBH) of stems over 1.3 m tall and 5 cm DBH. From these we determined: mean canopy height, ratio of stems over 1.3 m to stems over 5 cm DBH, mean DBH, and basal area. These four values were combined using Principal Components Analysis (PCA) with the package 'vegan' (ver 2.5.2; Oksanen et al. 2018), and the first two axes were used as metrics of vegetation structure in the modelling (Farina and Pieretti, 2014).

### 2.5. Modelling

Acoustic indices values cover widely different numeric ranges, and are frequently skewed. To permit comparison among indices, values were scaled by dividing by the maximum value of each index to give relative proportions. The NDSI is on a scale of −1 to + 1, so not amenable to this approach, therefore we used (NDSI + 1)/2 (Fairbrass et al. 2017). Normalised values were used as the response variable in a generalised mixed model framework with a beta distribution, conducted using the 'glmmTMB' package (ver 0.2.3; Brooks et al. 2017). The beta distribution is continuous between 0 and 1, but has no prior expectations related to the distribution within that range so can cope with asymmetric and heteroskedastic data (Ferrari and Cribari-Neto, 2004). Model predictors were mean bird species richness or mean abundance per site, and the first two PCA axes reflecting vegetation

structure. To account for potential autocorrelation, models included random effects for site, and day of deployment. The two avian metrics of species richness and abundance were co-linear so could not be included in a single model. Thus, we built two separate sets of models using either species richness or abundance, and then compared them using AIC to determine which was preferred (Burnham and Anderson, 2002).

## 3. Results

### 3.1. Bird and vegetation surveys

During point count surveys we detected a total of 4017 individual birds from 188 species. Mean bird species richness per site was 16.2 (range 5.5–25), and mean abundance per site was 23.4 (range 7.2–39.5). Vegetation structure differed among sites; forest habitats had taller canopies and greater basal area than scrub and pasture habitats (Appendix D). Axis 1 of the vegetation structure PCA accounted for 60.6% of the inter-site variance and reflected vegetation complexity; higher scores were associated with greater canopy height, basal area and mean DBH. Axis 2 accounted for 24.9% of the variance, and higher scores reflected a greater stem ratio; this was particularly marked in the plantation sites where intensive management reduces size variation among stems, with almost all stems part of the mature timber crop.

### 3.2. Soundscape, species richness and detections

Higher mean avian species richness and abundance from point count surveys were strongly associated with significantly higher values of ACI, AEve, Bio, NDSI and NDSI-Bio, and with significantly lower values of H and NDSI-Anthro (Fig. 3, Appendix E). Higher species richness was also significantly associated with lower ADI values, and higher abundance with greater values of M (Appendix E). AIC selection showed the mean species richness model was preferred for Bio, H, M, and the NDSI indices (Table E.3). For ACI, ADI and AEve there was no preference between mean species richness and mean abundance models, with delta AIC values of less than two.

Higher vegetation complexity scores on the first PCA axis were significantly associated with lower ACI values when added to both the species richness and abundance models, and with lower NDSI and higher NDSI-Anthro in the species richness model only (Tables E.1 and E.2). Axis 2 from the PCA, driven by changes in stem ratio, had a positive association with ACI in the species richness model.

## 4. Discussion

### 4.1. Relationships between biodiversity metrics and acoustic indices

Higher avian species richness and abundance were associated with higher values of ACI, AEve, Bio, NDSI and NDSI-Bio, and lower values of H, and NDSI-Anthro. Despite the correlation between richness and abundance, our models suggested that, overall, acoustic indices were more strongly related to species richness. In line with our hypotheses, sites with higher avian species richness and greater abundance have soundscapes with acoustic energy unevenly distributed among frequency bands. These patterns are evidenced by low ADI values and high Bio and NDSI-Bio values, which all indicate uneven distribution of acoustic energy among frequencies (Table B1). This is consistent with a greater number of birds emitting more calls that span a wider range of frequencies with greater temporal variation (Fig. 1b). Species-poor sites had impoverished soundscapes, with lower acoustic energy distributed more evenly across frequency bands (Fig. 1a). Critically, these patterns were coherent across the different indices, and across sites and habitats, emphasising the potential of acoustic indices for monitoring.

Some existing studies concur with our findings. A recent comparison of temperate and tropical recordings found correlations between species richness and the same indices we considered, emphasising that soundscape evenness declines with greater richness (Eldridge et al 2018). Similarly, Moreno-Gomez et al (2019) report similar associations between avian species richness and ADI and AEve. Although the direction of these correlations match our findings, both studies report only weak relationships in their tropical recordings, perhaps because the sparse recording schedules used meant there were insufficient data to demonstrate clear patterns (Bradfer-Lawrence et al. 2019). A strong positive association between the Bio index and bird abundance was found in Hawaii (Boelman et al. 2007), and in Papua New Guinea, less disturbed sites had soundscapes with greater acoustic saturation, due to either higher species richness or greater faunal abundance (Burivalova et al. 2018).

Our findings contrast with studies that suggest greater avian species richness, better “ecological condition” and lower disturbance are all associated with more even soundscapes (Sueur et al., 2008; Fuller et al 2015; Mammides et al 2017). We argue that methodological limitations may be responsible for variable findings in previous research, as they are counterintuitive given the soundscape patterns that underlie particular index values (Fig. 1). Habitats with rich faunal communities are likely to produce many different sounds at varied frequencies and timing intervals, leading to uneven soundscapes (Fig. 1b). In contrast, species poor sites are, on average, likely to have fewer vocalisations, and hence the soundscape will be more even (Fig. 1a).

Vegetation complexity significantly influenced ACI in both species richness and abundance models, and NDSI and NDSI-Anthro values in the species richness model only. Increasing vegetation complexity had the opposite effect to greater avian species richness and abundance on these indices values. The initially counter-intuitive relationship between ACI and vegetation complexity stems from the high ACI values in many of the pasture sites. High levels of tree cover (as remnant trees and living fences) in many Panamanian agricultural landscapes support a species-rich avifauna, and this is apparent in both the avian metrics and the acoustic indices. However, at the 20 m × 20 m vegetation plot scale, structural complexity is very low, leading to the apparent negative influence of vegetation complexity. The NDSI results may stem from more complex habitats having greater acoustic energy, irrespective of avian species richness or abundance. In more complex habitats there is a likely to be more biophony from birds and other fauna in the 1 – 2 kHz range that determines NDSI-Anthro values (Eldridge et al 2018). In turn, higher NDSI-Anthro values will reduce the ratio with NDSI-Bio, and thus cause lower overall NDSI.

Previous work has demonstrated further links between vegetation structure and acoustic indices. For example, in Costa Rica, ACI was correlated with liana abundance (Hilje et al 2017), and ADI with total vegetation complexity measured via LiDAR (Pekin et al., 2012). Higher levels of canopy cover have also been positively linked to Bio in Madagascar (Rankin and Axel, 2017). We ascribe the relatively low importance of vegetation in our findings to temporal factors. For example, over a time scale of 24 h, habitat type and vegetation structure are likely to define the potential range of acoustic indices values (Bradfer-Lawrence et al. 2019). However, when restricted to a 15-minute dawn chorus, indices values during an individual minute are more likely driven by vocalising fauna. This supports the use of acoustic indices for biodiversity monitoring, suggesting that by targeted sampling during the period of the day when the focal taxon is most vocal, indices values will be determined by the faunal assemblage rather than just reflecting broader habitat structure.

### 4.2. Using acoustic indices for biodiversity monitoring

Audio recordings can be collected at much greater spatial and temporal scales than most field data, and acoustic indices provide ready means of analysing these data, offering managers an additional method for monitoring biodiversity. For example, ACI has been used to time the arrival of migrant song birds on their breeding grounds (Buxton et al.

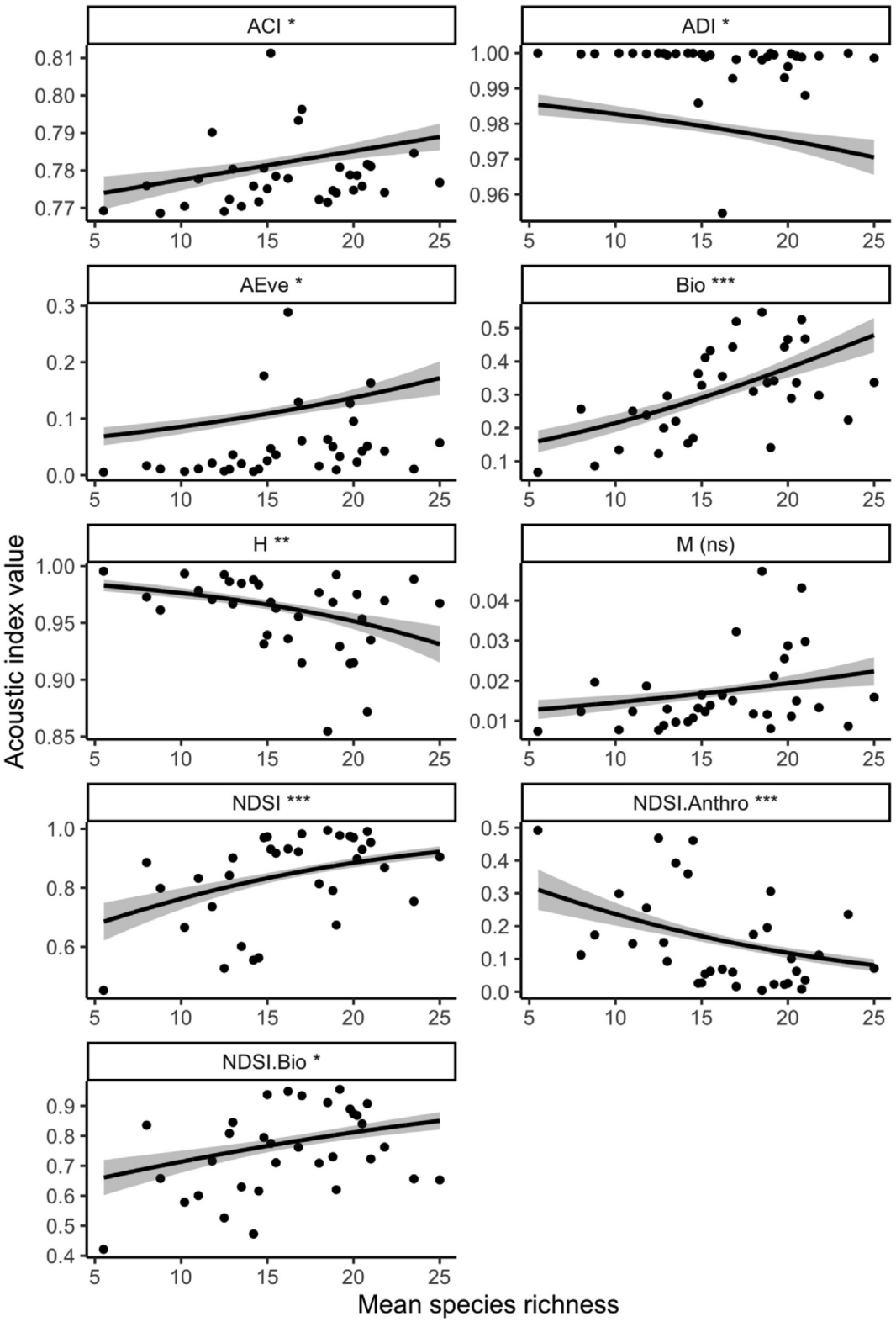


**Fig. 3.** Effect of mean avian species richness on normalised acoustic indices values, with median raw data as points, and predicted values and standard errors from generalised linear mixed models. Asterisks indicate significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Note raw data are highly skewed, and hence median points do not lie close to the predicted model fits for ADI and AEve; the long tail of the distributions are key to patterns in these indices.

2016). A large array of recorders across a region could be employed to track species arrival and relative abundance more readily than traditional survey methods, strengthening the evidence base for management decisions (Blumstein et al. 2011; Sugai et al. 2019). Similarly, the impacts of habitat fragmentation or restoration on animal species could be tracked across entire landscapes. Such a monitoring program could potentially highlight shifts in habitats and species at the landscape scale more rapidly than would be detected using field surveys, and so

facilitate management interventions (Gibbs and Breisch, 2001; Krause and Farina, 2016; Wood et al., 2019).

There are several important factors land managers should consider when using acoustic indices to monitor biodiversity. Successful use of acoustic indices must be grounded in a thorough understanding of which soundscape characteristics are reflected in changing values. Some acoustic indices are sensitive to geophony and anthrophony, and managers should be aware of potential influences on values, the options for pre-processing of recordings to minimise these influences, and the effects this processing might have on acoustic indices values. We demonstrated that greater avian species richness and abundance is associated with more uneven and complex soundscapes. Although we would expect similar soundscape patterns in other systems and with different taxa, land managers and conservationists would need to verify this anticipated link via ground-truth surveys (or manual checking of audio recordings) to establish faunal presence (Gibb et al 2018). With bird monitoring we recommend using mean avian metrics as site features rather than seeking to directly link acoustic indices values and bird surveys. High variability in calling rates and song types limits inference using the latter approach. Again, this pattern might apply with other taxa as well. If using formal statistical tests, we strongly encourage use of analysis techniques appropriate for skewed and bounded data.

Indices with the greatest range among sites were AEve, Bio and NDSI-Bio, suggesting these are potentially most sensitive to detecting spatio-temporal differences in faunal communities and so of greatest utility for monitoring. However, it is still valuable to include other indices that reflect different soundscape elements, as multiple indices offer insight into competing explanations. For example, high AEve values indicate a soundscape with energy unevenly distributed among frequency bands, which could reflect high levels of bird activity or complete dominance by insects such as cicadas. However, if ACI values are also high, this suggests rapid temporal variation lending support to the former interpretation (Pieretti et al. 2011; Bradfer-Lawrence et al. 2019). Some indices are also more robust to non-target noise; for example, ACI has been linked to biotic diversity even when there is substantial anthrophony (Duarte et al. 2015; Fairbrass et al. 2017).

New time- and cost-effective biodiversity monitoring methods are critically needed to provide evidence supporting robust policy decisions, habitat protection and conservation action (Eldridge et al 2018; Burivalova et al 2019a). Earlier failures to demonstrate consistent relationships between acoustic indices and other biodiversity metrics have meant practitioners are understandably reluctant to rely on these new monitoring tools (Browning et al 2017). Here we demonstrated that sites with higher avian species richness and abundance had consistently less even soundscapes, suggesting that acoustic indices can be used as effective conservation monitoring tools.

## CRediT authorship contribution statement

**Tom Bradfer-Lawrence:** Investigation, Methodology, Formal analysis, Writing - original draft. **Nils Bunnefeld:** Methodology, Formal analysis, Supervision, Writing - review & editing. **Nick Gardner:** Investigation, Writing - review & editing. **Stephen G. Willis:** Supervision, Writing - review & editing. **Daisy H. Dent:** Funding acquisition, Supervision, Writing - review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

We thank: the Autoridad de Canal de Panama and the private landowners who granted permission to deploy recorders on their land; the Autoridad Nacional del Ambiente for providing research permits (SE/A-134-16 and SE/A-67-18); the Smithsonian Tropical Research Institute for logistical support; Robbie Whytock and James Christie for helpful support with the Solo audio recorders; Scott Jackson for invaluable IT resources during indices calculations; Jeroen Minderman for valuable suggestions regarding the analysis; two anonymous reviewers for helpful comments that improved an earlier manuscript.

## Funding

TBL was funded by the Natural Environment Research Council UK, and the IAPETUS Doctoral Training Partnership (grant number 1672519).

## Data availability

Acoustic indices data and example sound recordings have been archived at DataSTORRE, the University of Stirling's online, publicly accessible repository for research data. Data set doi: http://hdl.handle.net/11667/148, Example recordings doi: http://hdl.handle.net/11667/147.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106400.

## References

Anderson, D.L., 2009. Ground versus canopy methods for the study of birds in tropical forest canopies: Implications for ecology and conservation. The Condor 111 (2), 226–237.

Bibby, C., Jones, M., Marsden, S., 2000. Expedition Field Techniques: Bird Surveys. BirdLife International. https://doi.org/10.1073/pnas.0809077106.

Blumstein, D.T., Mennill, D.J., Clemins, P., Girod, L., Yao, K., Patricelli, G., Deppe, J.L., Krakauer, A.H., Clark, C., Cortopassi, K.a., Hanser, S.F., Mccowan, B., Ali, A.M., Kirschel, A.N.G., 2011. Acoustic monitoring in terrestrial environments using microphone arrays: Applications, technological considerations and prospectus. J. Appl. Ecol. 48 (3), 758–767.

Boelman, N.T., Asner, G.P., Hart, P.J., Martin, R.E., 2007. Multi-Trophic Invasion Resistance in Hawaii: Bioacoustics, Field Surveys, and Airborne Remote Sensing. Ecol. Appl. 17 (8), 2137–2144.

Bradfer-Lawrence, T., Gardner, N., Bunnefeld, L., Bunnefeld, N., Willis, S.G., Dent, D.H., 2019. Guidelines for the use of acoustic indices in environmental research. Retrieved from. Methods Ecol. Evol. 10, 1796–1807. https://onlinelibrary.wiley.com/doi/abs/10.1111/2041-210X.13254.

Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9 (2), 378–400.

Browning, E., Gibb, R., Glover-Kapfer, P., Jones, K.E., 2017. Passive acoustic monitoring in ecology and conservation. Retrieved from. WWF Conservation Technology Series 2, 1–75. https://www.wwf.org.uk/conservationtechnology/documents/Acousticmonitoring-WWF-guidelines.pdf.

Burivalova, Z., Game, E.T., Butler, R.A., 2019a. The sound of a tropical forest. Science 363 (6422), 28–29.

Z. Burivalova Wahyudi Purnomo B., Boucher, T. M., Ellis, P., Truskinger, A., Towsey, M., Roe, P., Marthinus, D., Griscom, B., & Game, E. T. Using soundscapes to investigate homogenization of tropical forest diversity in selectively logged forests Journal of Applied Ecology 2019 10.1111/1365-2664.13481.

Burivalova, Z., Towsey, M., Boucher, T., Truskinger, A., Apelis, C., Roe, P., Game, E.T., 2018. Using soundscapes to detect variable degrees of human influence on tropical forests in Papua New Guinea. Conserv. Biol. 32 (1), 205–215.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Buxton, R., McKenna, M.F., Clapp, M., Meyer, E., Stabenau, E., Angeloni, L.M., Crooks, K., Wittemyer, G., 2018a. Efficacy of extracting indices from large-scale acoustic recordings to monitor biodiversity. Retrieved from. Conserv. Biol. 32 (5), 1174–1184. http://doi.wiley.com/10.1111/cobi.13119.

Buxton, R.T., Agnihotri, S., Robin, V.V., Goel, A., Balakrishnan, R., 2018b. Acoustic indices as rapid indicators of avian diversity in different land-use types in an Indian biodiversity hotspot. Journal of Ecoacoustics 2, GWPZVD.

Buxton, R.T., Brown, E., Sharman, L., Gabriele, C.M., McKenna, M.F., 2016. Using bioacoustics to examine shifts in songbird phenology. Ecol. Evol. 6 (14), 4697–4710.

Darras, K., Pütz, P., Fahrurrozi, Rembold, K., Tscharntke, T., 2016. Measuring sound

detection spaces for acoustic animal sampling and monitoring. Biol. Conserv. 201, 29–37. https://doi.org/10.1016/j.biocon.2016.06.021.
Duarte, M.H.L., Sousa-Lima, R.S., Young, R.J., Farina, A., Vasconcelos, M., Rodrigues, M., Pieretti, N., 2015. The impact of noise from open-cast mining on Atlantic forest biophony. Retrieved from. Biol. Conserv. 191, 623–631. https://doi.org/10.1016/j.biocon.2015.08.006.
Eldridge, A., Casey, M., Moscoso, P., Peck, M., 2016. A new method for ecoacoustics? Toward the extraction and evaluation of ecologically-meaningful soundscape components using sparse coding methods. Retrieved from. PeerJ 4, e2108. https://peerj.com/articles/2108.
Eldridge, A., Guyot, P., Moscoso, P., Johnston, A., Eyre-Walker, Y., Peck, M., 2018. Sounding out ecoacoustic metrics: Avian species richness is predicted by acoustic indices in temperate but not tropical habitats. Retrieved from. Ecol. Ind. 95, 939–952. https://doi.org/10.1016/j.ecolind.2018.06.012.
Fairbrass, A.J., Rennett, P., Williams, C., Titheridge, H., Jones, K.E., 2017. Biases of acoustic indices measuring biodiversity in urban areas. Retrieved from. Ecol. Ind. 83, 169–177. https://doi.org/10.1016/j.ecolind.2017.07.064.
Farina, A., Pieretti, N., 2014. Sonic environment and vegetation structure: A methodological approach for a soundscape analysis of a Mediterranean maqui. Ecol. Inf. 21, 120–132.
Farina, A., Pieretti, N., Piccioli, L., 2011. The soundscape methodology for long-term bird monitoring: A Mediterranean Europe case-study. Retrieved from. Ecol. Inf. 6 (6), 354–363. https://doi.org/10.1016/j.ecoinf.2011.07.004.
Ferrari, S.L.P., Cribari-Neto, F., 2004. Beta regression for modelling rates and proportions. Journal of Applied Statistics 31 (7), 799–815.
Fuller, S., Axel, A.C., Tucker, D., Gage, S.H., 2015. Connecting soundscape to landscape: Which acoustic index best describes landscape configuration? Retrieved from. Ecol. Ind. 58, 207–215. http://linkinghub.elsevier.com/retrieve/pii/S1470160X15003179.
Furumo, P.R., Aide, T.M., 2019. Using soundscapes to assess biodiversity in Neotropical oil palm landscapes. Retrieved from. Landscape Ecol. 34 (4), 911–923. https://doi.org/10.1007/s10980-019-00815-w.
Gage, S.H., Wimmer, J., Tarrant, T., Grace, P.R., 2017. Acoustic patterns at the Samford Ecological Research Facility in South East Queensland, Australia: The Peri-Urban SuperSite of the Terrestrial Ecosystem Research Network. Retrieved from. Ecol. Inf. 38, 62–75. https://doi.org/10.1016/j.ecoinf.2017.01.002.
Gibb, R., Browning, E., Glover-Kapfer, P., Jones, K.E., 2018. Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. Methods Ecol. Evol. 10 (2), 1–17.
Gibbs, J.P., Breisch, A.R., 2001. Climate warming and calling phenology of frogs near Ithaca, New York, 1900–1999. Conserv. Biol. 15 (4), 1175–1178.
Gómez, W.E., Isaza, C.V., Daza, J.M., 2018. Identifying disturbed habitats: A new method from acoustic indices. Retrieved from. Ecol. Inf. 45, 16–25. https://doi.org/10.1016/j.ecoinf.2018.03.001.
Hilje, B., Stack, S., Sánchez-Azofeifa, A., 2017. Lianas abundance is positively related with the avian acoustic community in tropical dry forests. Forests 8 (9), 1–12.
Jorge, F.C., Machado, C.G., da Cunha Nogueira, S.S., Nogueira-Filho, S.L.G., 2018. The effectiveness of acoustic indices for forest monitoring in Atlantic rainforest fragments. Retrieved from. Ecol. Ind. 91, 71–76. https://doi.org/10.1016/j.ecolind.2018.04.001.
Krause, B., Farina, A., 2016. Using ecoacoustic methods to survey the impacts of climate change on biodiversity. Retrieved from. Biol. Conserv. 195, 245–254. http://linkinghub.elsevier.com/retrieve/pii/S0006320716300118.
Laiolo, P., 2010. The emerging significance of bioacoustics in animal species conservation. Retrieved from. Biol. Conserv. 143 (7), 1635–1645. https://doi.org/10.1016/j.biocon.2010.03.025.
Lellouch, L., Pavoine, S., Jiguet, F., Glotin, H., Sueur, J., 2014. Monitoring temporal change of bird communities with dissimilarity acoustic indices. Methods Ecol. Evol. 5 (6), 495–505.
Mammides, C., Goodale, E., Dayananda, S.K., Kang, L., Chen, J., 2017. Do acoustic indices correlate with bird diversity? Insights from two biodiverse regions in Yunnan Province, south China. Retrieved from. Ecol. Ind. 82, 470–477. https://doi.org/10.1016/j.ecolind.2017.07.017.
Merchant, N.D., Fristrup, K.M., Johnson, M.P., Tyack, P.L., Witt, M.J., Blondel, P., Parks, S.E., 2015. Measuring acoustic habitats. Methods Ecol. Evol. 6 (3), 257–265.
Moreno-Gomez, F.N., Bartheld, J., Silva-Escobar, A. A., Briones, R., Márquez, R., Penna, M. (2019). Evaluating acoustic indices in the Valdivian rainforest, a biodiversity hotspot in South America. Ecological Indicators, 103, 1-8.
Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2018). vegan: Community Ecology Package. R package version 2.5-2.
Pekin, B.K., Jung, J., Villanueva-Rivera, L.J., Pijanowski, B.C., Ahumada, J.A., 2012. Modeling acoustic diversity using soundscape recordings and LIDAR-derived metrics of vertical forest structure in a neotropical rainforest. Landscape Ecol. 27, 1513–1522.
Pereira, H., Ferrier, S., Walters, M., Geller, G., Jongman, R., Scholes, R.J., Bruford, M.W., Brummit, N., Butchart, S.H.M., Cardoso, A.C., Coops, N.C., Dulloo, E., Faith, D.P., Freyhof, J., Gregory, R.D., Heip, C., Höft, R., Hurtt, G., Jetz, W., Karp, D.S., McGeoch, M.A., Obura, D., Onoda, Y., Pettorelli, N., Reyers, B., Sayre, R., Scharlemann, J.P.W., Stuart, S.N., Turak, E., Walpole, M., Wegmann, M., 2013. Essential biodiversity variables. Science 339, 277–279.
Pieretti, N., Farina, A., Morri, D., 2011. A new methodology to infer the singing activity of an avian community: The Acoustic Complexity Index (ACI). Ecol. Ind. 11 (3), 868–873.
Pijanowski, B.C., Villanueva-Rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M., Gage, S.H., Pieretti, N., 2011. Soundscape Ecology: The Science of Sound in the Landscape. Retrieved from. Bioscience 61 (3), 203–216. https://academic.oup.com/bioscience/article-lookup/doi/10.1525/bio.2011.61.3.6.
Rankin, L., Axel, A.C., 2017. Biodiversity Assessment in Tropical Biomes using Ecoacoustics: Linking Soundscape to Forest Structure in Human-dominated Tropical Dry Forest in Southern Madagascar. In: Farina, A., Gage, S.H. (Eds.), Ecoacoutics: The ecological role of sounds. John Wiley & Sons Ltd, Hoboken, NJ, pp. 129–144.
Ribeiro, J.W., Sugai, L.S.M., Campos-Cerqueira, M., 2017. Passive acoustic monitoring as a complementary strategy to assess biodiversity in the Brazilian Amazonia. Biodivers. Conserv. 26, 2999–3002.
Servick, K., 2014. Eavesdropping on Ecosystems. Science 343, 834–838.
Sueur, J., Aubin, T., Simonis, C., 2008. Seewave, a Free Modular Tool for Sound Analysis and Synthesis. Retrieved from. Bioacoustics 18 (2), 213–226. http://rug.mnhn.fr/seewave/PDF/Sueuretal_Bioacoustics_2008.pdf.
Sueur, J., Farina, A., Gasc, A., Pieretti, N., Pavoine, S., 2014. Acoustic indices for biodiversity assessment and landscape investigation. Acta Acustica United with Acustica 100 (4), 772–781.
Sueur, J., Farina, A., 2015. Ecoacoustics: the ecological investigation and interpretation of environmental sound. Biosemiotics 8 (3), 493–502.
Sugai, L.S.M., Desjonqu, C., Silva, T.S.F., Llusia, D., 2019. A roadmap for survey designs in terrestrial acoustic monitoring. Remote Sens. Ecol. Conserv. 1–16. https://doi.org/10.1002/rse2.131.
Tucker, D., Gage, S.H., Williamson, I., Fuller, S., 2014. Linking ecological condition and the soundscape in fragmented Australian forests. Landscape Ecol. 29 (4), 745–758.
Villanueva-Rivera, L.J., Pijanowski, B.C., 2018. soundecology: Soundscape Ecology. R package version 1 (3), 3.
Whytock, R.C., Christie, J., 2017. Solo: an open source, customizable and inexpensive audio recorder for bioacoustic research. Methods Ecol. Evol. 8 (3), 308–312.
Windsor, D. M. (1990). Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. Smithsonian Contributions to the Earth Sciences (Vol. 29). Washington D.C.
Wood, C.M., Popescu, V.D., Klinck, H., Keane, J.J., Gutiérrez, R.J., Sawyer, S.C., Peery, M.Z., 2019. Detecting small changes in populations at landscape scales: a bioacoustic site-occupancy framework. Retrieved from. Ecol. Ind. 98, 492–507. https://doi.org/10.1016/j.ecolind.2018.11.018.
Zhao, Z., Xu, Z., Bellisario, K., Zeng, R., Li, N., Zhou, W., Pijanowski, B.C., 2019. How well do acoustic indices measure biodiversity? Computational experiments to determine effect of sound unit shape, vocalization intensity, and frequency of vocalization occurrence on performance of acoustic indices. Retrieved from. Ecol. Ind. 107, 105588. https://doi.org/10.1016/j.ecolind.2019.105588.